
Report 2:

SPATIAL TRENDS IN COMMUNITY AND HEALTH-RELATED CHARACTERISTICS OF GALVESTON BAY OYSTER REEFS

By

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Introduction

Oysters are generally considered to do best at moderate salinities (12-20 ppt). Factors restricting oyster production outside this salinity range include increased respiratory demand, decreased filtration rate and mortality at lower salinity and predation and disease at higher salinity (Powell et al., submitted a, Hofmann et al., submitted; Powell et al., in press). Production on reefs, however, is significantly affected by variables like food supply and rate of recruitment that might follow salinity in a more complex way. For example, lowered food concentrations, regardless of salinity, may increase infection intensity of *Perkinsus marinus*, an important source of mortality in oyster populations of the Gulf coast, and reduce growth, fecundity and survivorship of the oyster population. In addition, the direct affect of the commercial fishery is poorly known. Some reefs are heavily fished, others less so, in the same salinity regime (Quast et al., 1988). For example, to the extent that fishing is a compensatory source of mortality, fishing may reduce *P. marinus* infection intensity by selectively reducing the abundance of the most heavily-infected portion of the population. Accordingly, the productivity of oyster populations might not be a simple function of salinity, and, indeed, the accompanying survey of reef accretion and loss over a 20 year interval in Galveston Bay did not reveal a clear trend with the prevailing salinity gradient over that time. Moderate salinity areas, on the average, accreted more new reef, however areas of similar salinity accreted and lost reef area during this time over much of the salinity gradient in the bay.

In May, 1992, a survey was conducted of the oyster population, community and health-related characteristics of oyster reefs in Galveston Bay, Texas. This survey provides the opportunity to differentiate the effects of salinity from other sources of variability in determining the population and community structure of oyster reefs

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within the salinity gradient and their relative health as measured by population and disease-related attributes like size-frequency composition, *P. marinus* prevalence and infection intensity, and gonadal state.

Methods

Field sampling

A depiction of the Galveston Bay system showing important geographic features, locations of reef accretion and loss, and important physical characteristics is provided on page 177 in the Map Appendix of this report and as Map Set 19 in Map Atlas: Volume II. Samples were taken over a period of 3 weeks in April-May 1992 by the R/V Eddy. The sampling period occurred during flood conditions on the Trinity River, the primary freshwater source for Galveston Bay. Salinities were near record lows in many locations and had been for a period of at least 4 months prior to sampling (our unpublished data). Accordingly, certain population characteristics, like gonadal index and *P. marinus* prevalence and infection intensity, were recorded during a period of time when environmental conditions would have minimized their values over much of the bay system.

Reef sampling sites are listed in Table 1 and on page 179 in the Map Appendix of this report and as Map Set 20 in Map Atlas: Volume II. Stations sampled include (1) commercially open and closed reefs, (2) reefs of varying form such as barrier reefs, alongshore reefs and patch reefs, (3) reefs covering a wide range of salinity and current flow, and (4) reefs in areas of net reef accretion and loss over the last 20 years. Sites were chosen using the accompanying oyster reef survey of Galveston Bay and their GPS positions recorded. At each site, one to four measured dredge hauls were taken. The dredge used was a 12-toothed dredge of Louisiana design, 68 cm in mouth opening, towed along a straight line from a position aft at the level of the gunnels, about two feet above the water line. To maintain proper aspect while dredging, 10 feet of line were laid out for each foot of depth and a length of heavy chain was added between the line and the dredge. Dredging speed was generally less than 1 knot. Distance was determined using a precision range finder from the boat to a buoy dropped on the reef, so that areal coverage could be estimated. Dredging efficiency declined if the dredge was towed downslope. Accordingly, depth of bottom was recorded frequently during each tow and only tows alongslope or upslope were used. Dredging efficiency also improved when towed 90° or less to windward. Accordingly, where possible, all tows were made some degree to windward.

Use of measured dredge hauls allowed us to correct for varying areas covered, a source of significant error when timed dredge hauls are used. Accordingly, data were normalized to area covered by the dredge, assuming dredging efficiency was constant throughout the study. Dredging efficiency was estimated by Medcof (1961) to range as high as 30%. Chia et al. (1992) recorded efficiencies between 2% and 32%. We estimated from our data and comparison to data obtained by Soniat and Brody (1988) and Soniat (1982) from the same sites that our efficiency ranged

around 12%, however short-term changes in weather and site-related factors certainly affected efficiency from site to site. Consequently, the values reported are not corrected for dredging efficiency but are corrected for the area sampled by the dredge.

Laboratory Analyses - population parameters

Shell volume collected was estimated from displacement volume. All shell collected regardless of condition was included. The longest dimension of the 10 largest clumps was measured. The number of boxes was recorded. All live oysters were measured (anterior-posterior length), and their wet meat weight recorded. Dry weight was estimated using the conversion of Choi et al. (1993). Individuals were divided into 3 size groupings: juveniles (< 50 mm), submarket-size adults (50 - 76 mm) and market-size adults (> 76 mm). All significant predators were identified and measured. In practice, significant predators were crabs of a variety of species and the oyster drill *Thais haemastoma*. Apex-adapical length was measured for *Thais* and carapace width for the crabs.

Selected common epibionts and endobionts were enumerated. Mussels (*Brachidontes* spp.) were counted and their anterior-posterior length measured. Barnacles, bryozoans and algae were estimated by areal coverage (0-10%, 10-30%, 30-50%, 50-75%, > 75%). Polychaetes were removed by dissolving the shell in a decalcifying fluid (Gittings et al., 1984) and weighing the individuals present.

Laboratory Analyses - individual parameters

Condition index was calculated from tissue dry weight and mantle cavity volume measured by displacement before and after shucking. A condition code rating (Quick and Mackin, 1972) was given to each oyster immediately after opening. The amount of gonadal tissue present was assessed quantitatively by single ring immunodiffusion assay in females using the method of Choi et al. (1993) as described in detail by Choi and Powell (in press). A gonadal-somatic index was calculated as mg dry wt egg mg dry wt somatic tissue⁻¹. Sex was determined by examining a smear slide.

Perkinsus marinus was assessed semiquantitatively by Ray's (1966) method as described by Wilson-Ormond et al. (in press). Because the study was done during a period of low salinity, many false negatives were recorded. Accordingly, a subset of individuals was examined using the quantitative method of Choi et al. (1989) as described by Wilson-Ormond et al. (in press) to better define prevalence and infection intensity in lightly infected populations. Prevalence was calculated as percent infected, using the quantitative data where required. Mean infection intensity was calculated using the semiquantitative scale of Mackin (1962) as described by Wilson-Ormond et al. (in press).

Statistics

The following primary data were used for cluster analysis: maximum clump size (mean in mm), juvenile oysters (ind m⁻²), submarket-size oysters (ind m⁻²), market-size oysters (ind m⁻²), biomass (g m⁻²), prevalence of *P. marinus* (%), mean infection intensity (mean of Mackin's number), mussels (ind m⁻²), crabs (ind m⁻²), *Thais* (ind m⁻²), shell volume (l m⁻²), boxes (ind m⁻²), condition index (mean of g dry wt ml⁻¹), eggs present (mean of mg ind⁻¹), GSI (mean of mg dry wt egg mg dry wt somatic tissue⁻¹), polychaetes (mean of total weight oyster⁻¹), barnacles (mean of % coverage), bryozoans (mean of % coverage), algae (mean of % coverage). Raw data were normalized to m⁻² where appropriate, as just shown, using the area covered by the dredge obtained from the known mouth opening and the distance traveled. All data categories were internally standardized to parts per thousand and log-transformed (Boesch, 1977). The cluster program used an unweighted pair-group algorithm with Euclidean distance as the similarity index (Boesch, 1977). No further information was obtained when the data were further normalized to the shell volume collected.

The spatial distribution of each variable was examined using a spatial autocorrelation method described by Cliff and Ord (1973). We used Moran's I as the test statistic, where

$$I = (n/W) \frac{\sum_{i=1}^n \sum_{\substack{j=1 \\ i \neq j}}^n w_{ij} z_i z_j}{\sum_{i=1}^n z_i^2}$$

and

$$W = \sum_{i=1}^n \sum_{\substack{j=1 \\ i \neq j}}^n w_{ij}; \quad z_i = x_i - \bar{x};$$

n = number of samples; x_i = datum of sample i ; and w_{ij} = a weighting measure as described below.

Moran's I is sensitive to the location of extreme departures from the mean ($x_i - \bar{x}$). In a patchy population, adjacent samples would both tend to be much above or below the mean more frequently than would be expected by chance. Cliff and Ord (1973) showed, for samples that are spatially randomly distributed, that the expected value of I is $-(n-1)^{-1}$ (≈ -0.02 in this study). Hence, values of I below $-(n-1)^{-1}$ indicate negative spatial autocorrelation (an even distribution) and values above

$-(n-1)^{-1}$ indicate positive spatial autocorrelation (a patchy distribution). Significance levels were calculated after Jumars et al. (1977) under the assumption of randomization.

The use of this technique depends upon the choice of a weighting system (w_{ij}) which is a mathematical expression of the spatial relationship between the sampled sites. Following Wilson et al. (1992), we constructed a Gabriel-connected graph (Gabriel and Sokal, 1969) for the sites (on page 179 in the Map Appendix of this report and as Map Set 20 in Map Atlas: Volume II). In this case, two sites (\overline{AB}) were considered connected if no third site (C) existed that formed an obtuse angle when connected between the other two ($\angle ACB$). Sokal and Oden (1978a) discuss occasions eliciting modifications in a Gabriel graph. In this case, we deleted from the analysis site pairs that were linked by overland connections because population interactions by larval transport could not have directly occurred between these sites.

The change in spatial relationship among samples at varying distances can be used to identify the scale of spatial variation. For example, in a patchy population, samples closer than patch size will be more similar than expected by chance [e.g. Moran's $I < -(n-1)^{-1}$]. We examined the change in spatial relationship using two approaches. (1) We examined the change in spatial relationship with distance using correlograms (plots of sample similarity versus distance between samples) calculated as discussed by Sokal and Oden (1978a,b). Distances were calculated along the Gabriel network by Marble's method (1967). Sites within a given distance from one another when joined along the Gabriel network were given a weight (w_{ij}) of 1.0; for all others $w_{ij} = 0$. Therefore, these correlograms were distance-corrected using the terminology of Sokal and Oden (1978a). (2) We also examined the change in spatial relationship with compass direction [directional spatial autocorrelation of Sokal et al. (1987)]. In this case, correlograms were generated from north northeast (22.5°) to south (180°) in 22.5° intervals. [Values from south southwest (202.5°) to north (360°) would be identical and so, for brevity, are not included.] For each interval, a weight was calculated for each Gabriel pair as the fractional deviation of the angle between the site pairs from the preferred angle for that interval, calculated as $\sin(\alpha)$. So, if the preferred angle were 90° , two sites exactly east-west would have received a weight (w_{ij}) of 1.0; two sites exactly north-south (180°) would have received a weight of 0, and two sites southeast-northwest (135°) of each other would have received a weight of 0.71. Unlike Sokal et al. (1987), we did not include distance between sites in the analysis. However, only site pairs directly linked in the Gabriel network without intervening sites were included in the analysis, so the resulting correlogram considers only those sites very near to each other in spatial arrangement.

To estimate the distribution of variables among all reefs in Galveston Bay, we utilized the division of the bay into 1996 elements or sections as defined by the Army Corps of Engineers hydrodynamic model (Berger et al., 1992). This grid plan is shown in Figure 1. These elements provided a detailed division of the bay's area which was also used in model simulations as described later; hence it was convenient to use this division scheme for all purposes. Each element is a

quadrilateral defined by a set of corner nodes (4 for a rectangle). We assigned the measured variable to each of the corner nodes of an element containing a sampling site. Distances (D_{ij}) were calculated from each defined node to all other nodes (> 5000 corners in the 1996-element grid) using Marble's (1967) method. The value for each unknown node (U_j) was obtained as the distance-corrected mean of the known nodes (K_i) where

$$U_j = \sum_i^{51} [(1/D_{ij}^2) / \sum_i^{51} (1/D_{ij}^2)] K_i$$

The variable value for each undefined (unsampled) element was then obtained as the mean of the corner nodes.

Computer simulations were run for each element using the TAMU/ODU oyster population dynamics model (Table 2), components of which are described by Powell et al. (1992, in press, submitted a,b), Dekshenieks et al. (in press) and Hofmann et al. (submitted). Flow fields and salinities were obtained using the Army Corps of Engineers Galveston Bay finite element hydrodynamic model for conditions defined by mean monthly river flows averaged over the last 40 years (Berger et al., 1992). A temperate time series for an average year (1984) was obtained from NOAA (1984). Conditions similar to these occur in Galveston Bay in about 60% of the years. Food and turbidity data came from our own unpublished data obtained as described by Powell et al. (submitted b). The remaining variables initializing the model (e.g. *P. marinus* prevalence) were obtained from the present data set with the exception of oyster density and size frequency. We used a typical density and size frequency for Confederate Reef as described by Powell et al. (submitted a) for each element to aid in comparison. Thus, each section of the bay began with an identical oyster population in terms of density and size frequency. The simulation was run for two years and the second year's results used for interpretation.

Results

Primary data

Salinity was low, usually below 10 ppt, over most of the bay during the sampling period (Table 1). Relatively high salinity was recorded in all West Bay sites and at sites near Bolivar Roads in Galveston Bay proper. Much of Trinity Bay was near 0 ppt.

More shell was obtained per m² dredged in the Redfish Bar area and along the Houston Ship Channel than elsewhere (Table 3, Figs. 1, 2). Lowest values obtained were at the extremes of the salinity gradient in lower West Bay, upper East Bay and upper Trinity Bay. The amount of shell collected was not obviously related to the areas of reef accretion and loss described in the accompanying reef survey. Overall, although not entirely, areas having highest shell volumes were in areas

open to commercial fishing (TDH, 1992). Either shell was more plentiful in these areas or shell was less consolidated and more easily picked up by the small dredge used for this survey in these areas. Partial correlation coefficients were calculated from the best 4-variable model. Many of the variables considered are themselves correlated, so the results of this analysis must be used only descriptively. Nevertheless, shell volume correlated best with oyster biomass, number of boxes, and juvenile abundance (Table 4).

Overall, the largest clumps obtained were taken from West Bay, the South Redfish Reef area of Redfish Bar, the Red Bluff area, and upper East Bay (Table 3, Figs. 2, 3). These areas include both those closed to the fishery and open to the fishery during the winter fishing season. They also include closed areas typically fished during the summer relay program and areas rarely fished at all. Accordingly, the possibility that continual dredging and culling results in a less consolidated reef surface is not borne out by the survey. Clump size was significantly correlated with the abundance of market-size oysters and mean *P. marinus* infection intensity (Table 4).

Highest oyster densities were found in the Redfish Bar area of Galveston Bay and on the reefs west and south of Smith Point (Gaspice Reef, Barts Pass Reef) (Table 3, Figs. 2, 4). Local abundance highs also occurred in the Deer Island area of West Bay, the Red Bluff area of Galveston Bay, and lower Trinity Bay (Tern Reef). Oyster density also averaged high along the Houston Ship Channel, except in the Morgans Point reach. Assuming a dredging efficiency of 12%, highest true densities averaged between 50 and 100 oysters m⁻². These values are low compared to literature values from some other areas (Dame, 1976; Moore, 1907; Moore and Danglade, 1915), but probably relatively typical for Galveston Bay (Soniati and Brody, 1988). Soniat et al. (1989) reported densities from 16 reefs in Galveston Bay. Our values for these same areas, assuming a 12% dredging efficiency, show lower densities than observed by Soniat et al. (1989) (Table 5). To some extent, however, this is a misleading statistic because many of the reefs sampled by Soniat et al. (1989) were in low salinity areas of the bay which, during our study period, had seen salinities below 5 ppt for nearly 6 months.

Juvenile oysters were most abundant along the Houston Ship Channel, on and near Redfish Bar, and west of the Houston Ship Channel above Todds Dump. Lowest values were in the Dickinson Embayment, East Bay and Trinity Bay (Table 3). Some West Bay samples were dominantly or entirely composed of juveniles. Market-size oysters essentially followed the trends noted for all oysters (Figs. 2, 5, Table 3). Submarket-size oysters were most abundant in Trinity Bay, west of the Houston Ship Channel above Todds Dump, and in the Redfish Bar area (Table 3). The abundance of submarket-size oysters in the latter two areas probably originates from heavy recruitment within the previous year, whereas the abundance in Trinity Bay may also be due to regional stunting in adult size. The abundance of juvenile oysters was significantly correlated with the abundance of submarket-size oysters, gonadal-somatic index, and mean infection intensity (Table 4). The abundance of market-size and submarket-size oysters, not surprisingly, were correlated with biomass. The abundance of market-size oysters were also inversely correlated with the abundance of mussels. As many of the variables in the regression analysis are

themselves correlated, these results can only be used to suggest that some relationships between variables may be more important than others.

Oyster size-frequency (Fig. 6) varied significantly from site to site; however, no trends between regions or across salinity regimes could be discerned, with one exception. Sites dominated by juveniles were largely confined to West Bay and the Pelican Island Embayment. With the exception of the Deer Island area, few adults were collected at sites in this region. Although Chi-square tests uncovered significant differences between sites, grouping data by salinity, fishing status, or region did not produce significant differences unexplained by local variation. Simulations of Galveston Bay oyster populations (see later discussion) show that important local variations in oyster production exist which would compromise the statistical treatment of sites grouped by larger regions or by salinity.

With one exception (Pepper Grove Reefs), oysters of 90 cm or larger were rarely obtained. This rarity included fished and unfished reefs, reefs in all salinity regimes, and all areas of the bay. Powell et al. (submitted b) suggested that Galveston Bay, as a whole, has a food supply insufficient to support many oysters of this size. The field data support the contention of Powell et al. (submitted b) that food supply in Galveston Bay is just barely adequate to support a market-size population.

Oyster biomass (Table 3, Figs. 2, 7) was high on Redfish Bar, between Redfish Bar and Smith Point, and off Red Bluff. Lowest biomass were generally at sites at the salinity extremes: central West Bay, upper East Bay, upper Trinity Bay, and Morgans Point. Biomass was not associated with fishing status and substantial local variation was present. Reefs less than 2 miles apart had significantly different biomass. Along the Houston Ship Channel, biomass was low in the reach above Buoy 75, peaked on Redfish Bar in the reach from Buoy 63 to Buoy 53, and then declined towards Bolivar Roads. Generally, biomass declined east and west of the ship channel as well.

Oyster growth form is plastic. Kent (1988) proposed that growth form is related to habitat. Variation in growth form would result in variation in meat weight for a given shell length, as most changes in growth form change the length/width ratio of the shell. Most adult oysters collected ranged up to 3 g dry wt in size. A few were as heavy as 6 g dry wt. Figure 8 shows that substantial variation exists between sites in the length/meat weight relationship among sites. Over the range of sites sampled, a market-size oyster (76 mm) could range from about 7.5 g wet wt (1.7 g dry wt) to nearly 30 g wet wt (6 g dry wt). Length-biomass relationships did not vary predictably with salinity, fishing status or bay region. Reef-to-reef variation predominated.

These data emphasize the danger of basing management decisions on a linear determination for the size-frequency distribution. Most biological variables, like fecundity, vary with weight rather than length and so could vary by a factor of 5 for a given shell length in the market-size size classes. Furthermore, the failure of some reefs to support the larger biomass size classes might not be obvious based on length. For example, Tern Reef had some of the longest oysters obtained during the

study, however meat weights were relatively low. Yacht Club Reef, with much shorter oysters, actually supported a much larger biomass.

Boxes were rare at most sites (Fig. 2). Most boxes were collected from sites within the primary discharge route of Trinity River water through Galveston Bay (depicted on page 177 in the Map Appendix of this report and as Map Set 19 in Map Atlas: Volume II). The Trinity River was at flood stage during our sampling. Recent mortality caused by low salinity was observed at Vingt-et-un Reef and Possum Pass Reef and probably had occurred at these other locations. The distribution of boxes recorded by Soniat et al. (1989) differed substantially from this study. Soniat et al. (1989) sampled during a more normal year and their study took place somewhat later in the season when *P. marinus* mortalities may have been occurring on some reefs. Boxes were much more common in our study on low salinity reefs than observed by Soniat et al. (1989) in accordance with suspected or observed (Vingt-et-un Reef) low salinity-induced mortalities (Table 5).

Condition index for market-size oysters was calculated after Soniat et al. (1989) ($\text{g dry wt ml}^{-1} \times 100$). Average condition index ranged from 9.75 in Trinity Bay to 14.34 on the west side of the Houston Ship Channel (Table 3, Figs. 2, 9). Most areas of the bay, however, showed similar condition indices. In contrast, nearby reefs frequently differed considerably in condition index. Condition index varied significantly with salinity and significantly inversely with gonadal-somatic index and clump size (Table 4). No relationship with fishing status could be discerned. In general, the values obtained for condition index in this study were about double the values obtained by Soniat et al. (1989) (Table 5). Sampling earlier in the reproductive season is the probable explanation for this discrepancy.

Gonadal-somatic index is a quantitative measure of the development of gonadal material. Female oysters were collected on only two reefs in Trinity Bay and at only three sites in West Bay. The former was probably due to low salinity inhibiting reproduction. The latter was due to the predominant collection of juveniles at some sites. Considering the remaining sites, gonadal-somatic index was highest in the middle of the salinity range: the Dickinson Embayment, Redfish Bar, East Bay, and along the Houston Ship Channel (Table 3, Figs. 2, 10). Gonadal-somatic index was lowest at the extremes of the salinity range: West Bay, Trinity Bay, and the Morgans Point reach of the Houston Ship Channel. Gonadal-somatic index was significantly correlated with salinity (Table 4) and the abundance of juveniles and inversely correlated with mean infection intensity of *P. marinus*.

Only one previous study quantifying gonadal-somatic index is available for Galveston Bay. Those data, collected by Choi et al. (1993) in April 1989 were taken from Confederate Reef in West Bay and can be compared to our data from the Deer Island sites (Table 6). Even though oysters collected in the present study had about three times the biomass of those collected by Choi et al. (1993), mean gonadal-somatic index was less than 50% of the 1989 value in 1992. Even though some oysters collected in 1989 did not have developing gonads, gonadal-somatic indices ranged substantially higher in 1989 (up to 0.422) as well as averaging higher. The highest value recorded in this study was 0.144. Low salinities early in 1992 are one

possible explanation. Unfortunately, comparative data on food supply are not available.

Sex ratio varied considerably, from 0 (no females) to 9 (9 times more females than males) (Table 3). On the average females were proportionally more common in the higher salinity parts of the bay, however the variability between adjacent sites was generally high.

Prevalence of *P. marinus* was highest in parts of West Bay, however prevalence was generally above 50% (Table 3, Figs. 2, 11). These prevalences are relatively low in comparison to historic levels (e.g. Wilson et al., 1990; Powell et al., 1992; Soniat et al., 1989; Hofstetter, 1977) because of the unusually low salinity conditions present for the 4 months prior to our sampling. A comparison to NOAA's Status and Trends data demonstrate this trend (Table 7). The Status and Trends samples were taken during December or January of each year when prevalence and infection intensity would be expected to be lower than during the April and May period supplying the present data. Prevalence was not significantly correlated with any variable (except infection intensity). The failure of prevalence to correlate with other variables is not uncommon along the Gulf of Mexico coast (e.g. Powell et al., 1992). Factors controlling transmission rate are poorly understood (Hofmann et al., submitted) and recent community history is an important determinant (Powell et al., submitted a) not taken into account by simple regression analyses.

False negatives are frequently recorded with the conventional thioglycollate method when infection intensity is low. The average prevalence over the entire bay was just 12.9% using the standard thioglycollate method. Figure 12 compares prevalences using the quantitative method of Wilson et al. (in press) and the semiquantitative method of Ray (1966). Further assessing putative negatives using the quantitative method raised prevalence for the entire bay to 53.3%. Of additional note, only a weak correlation existed between the two determinations. That is, sites with low true prevalence, assessed quantitatively, and sites with high true prevalence, were just about as likely to show low prevalence by the semiquantitative technique. The explanation for this phenomenon lies in the low infection intensities found during the sampling period at sites with high prevalence. Many very light infections were judged negative by the standard thioglycollate assay.

P. marinus infection intensity was highest in West Bay (Table 3, Figs. 2, 13), however infection intensities were generally low in keeping with the time of year when sampling was conducted. Mean infection intensity was correlated with salinity (Table 4). Infection intensities were much lower in our study than noted by Soniat et al. (1989) (Table 5), Hofstetter (1966, 1977, 1983), or Hofstetter et al. (1965). Hofstetter (1977) recorded that most average yearly infection intensities for 1962 through 1972 varied between 1 and 3. Baywide averages recorded by NOAA's Status and Trends Program from 1986 to 1992 for the winter months never averaged as low as seen in our sampling (Powell et al., 1992; our unpublished data). Sampling during a period of much lower than average salinity explains our lower infection intensities.

Hofmann et al. (submitted) and Powell et al. (submitted a) concluded that a simple increase in infection intensity as a function of size or biomass frequently does not exist in infected oyster populations because of unpredictable larval settlement sporadically adding uninfected oysters, a more rapid disease intensification in smaller individuals, and variations in infection-produced mortality among individuals of different size. Although newly settled spat are uninfected, transmission rates are rapid enough that many individuals will become infected within a few months of settlement, but transmission rate is not necessarily dependent upon the rate of juvenile growth. Furthermore, smaller individuals require fewer population doublings of the parasite population to reach a given infection intensity. Accordingly, the larger size classes may not always be the most heavily-infected individuals nor may they always be representative of the entire population, even though they are the normally-sampled size class for the thioglycollate assay.

In Figure 14, we provide four examples of the relationship between infection intensity and length or biomass, chosen from three different regions of the bay. Correlations are poor, as anticipated from Hofmann et al. (submitted). Powell et al. (submitted a) argued for the necessity of measuring *P. marinus* prevalence and infection intensity throughout the size-frequency spectrum of oyster populations to adequately evaluate the disease process. Our data (Table 8) show that substantial variation in prevalence and infection intensity between size classes is the rule rather than the exception. Sole dependence on the market-size classes for analysis, as is the rule for these assays, may seriously underestimate or overestimate infection intensity in the entire population.

Thais haemastoma was only collected in West Bay and on Half Moon Reef in Galveston Bay. This distribution is considerably more restricted than that noted by Hofstetter (1977) due to two consecutive years of unusually low salinities. Crabs were collected on all reefs (Table 3, Figs. 2, 15). Most crabs collected were mud crabs (*Petrolisthes armatus*, *Panopeus herbstii* and *Eurypanopeus depressus*). Highest crab densities were recorded in West Bay, the southwestern portion of Redfish Bar to Smith Point, and in the Red Bluff area. Lowest abundances occurred in most reaches of the Houston Ship Channel, Trinity Bay, East Bay and in the Dickinson and Clear Lake Embayments. The number of crabs was correlated with oyster biomass and *P. marinus* mean infection intensity and inversely correlated with condition index (Table 4). No simple correlation with salinity existed, nor was fishing status important.

The carapace width size-frequency distributions for the crabs collected are shown in Figure 16. Most crabs collected had carapace widths of 10 mm or less. Larger crabs were collected at a few scattered sites such as South Deer Island Reef and Bull Shoals Reef. Larger crabs were not obviously associated with open or closed reefs, with a particular salinity regime, or with particular areas of the bay. Although Chi-square tests uncovered significant differences between sites in crab size-frequency distributions, grouping data by salinity, fishing status, or region did not produce significant differences unexplained by local variation.

Highest mussel density was observed on Yacht Club Reef (Table 3, Figs. 2, 17). Lowest mussel densities were observed in West Bay and along the Houston Ship Channel. Highest densities were observed in northern East Bay, Trinity Bay, and the western part of Galveston Bay from the Clear Lake Embayment to Morgans Point. In general, as has been noted elsewhere (Moore and Danglade, 1915; Moore, 1907), mussels were more abundant at lower salinity sites. This relationship appeared to be a step function with sites having salinities less than 14 ppt normally characterized by high mussel densities and sites having salinities above 14 ppt usually having few mussels. Mussels were significantly correlated with oyster biomass and inversely correlated with the abundance of market-size individuals (Table 4). No significant correlation occurred with salinity in the regression analysis because the relationship with salinity was nonlinear.

Most mussels were also small, less than 20 mm (Fig. 18). Some reefs had a larger proportion of large mussels, like Tern Reef, Todd's Dump, Buoy 63, and April Fools Reef. Larger mussels were not obviously associated with open or closed reefs, with a particular salinity regime, or with particular areas of the bay. Nor were large mussels found primarily on reefs having small or few crabs. Although Chi-square tests uncovered significant differences between sites, grouping data by salinity, fishing status, or region did not produce significant differences unexplained by local variation. Accordingly, the factors affecting the size-frequency distributions of mussels could not be identified.

Barnacle encrustation was highest in the moderate to low salinity regions of the bay as may be typical for Texas bays (e.g. Moore and Danglade, 1915). Bryozoan growth was highest in the high salinity regions of the bay, particularly West Bay and the Dickinson Embayment. Polychaetes were common only in West Bay. Algal coverage was high only in West Bay and from the Clear Lake Embayment to Morgans Point west of the Houston Ship Channel. Overall, epibionts and endobionts followed predictable salinity trends with one exception. Epibiont and endobiont growth was unusually low along the Houston Ship Channel. More rapid oyster growth rates in these areas is a possible explanation (e.g. Warburton, 1958). Only bryozoan coverage was significantly correlated with salinity. Polychaete, algae and mussel coverage were themselves significantly correlated, but none of these three were significantly correlated with salinity (Table 4). Barnacle coverage was not significantly correlated with any parameter. In all likelihood, the unusually low coverage at Houston Ship Channel sites explains the poor correlations of these variables with salinity.

Cluster analysis and autocorrelation

Stations clustered primarily by salinity (Fig. 19). Secondary groupings occurred by region along the salinity gradient. For example, Groups 1, 2, 3, 6, 7 and 8 were moderate salinity sites that generally divided according to bay region. Groups 1, 2, and 3 fell on either side of the primary route of outflow of Trinity River water across the Hanna Reef Tract (see page 177 in the Map Appendix of this report or Map Set 19 in Map Atlas: Volume II). Groups 6, 7, and 8 generally fell within the Trinity River plume across the same central section of the bay. These latter three groups

clustered in a more or less upstream-downstream orientation. Groups 4 and 5 were low salinity sites in East and Trinity Bays that clustered separately from the low salinity sites west of the Houston Ship Channel, Group 10. High salinity sites were divided between the productive region in easternmost West Bay, Group 9, and the depauperate areas of central West Bay and the Pelican Island Embayment, Group 12. Group 11 consisted of the two sites suffering flood-induced mortalities just prior to collection. Under normal conditions, these sites probably would have fallen into Groups 7 or 8. No groups distinctly distinguished sites by their fishing status: open versus closed.

Correlograms were used to identify scales of similarity and dissimilarity in the measured variables. As expected for environmental variables, stations further and further apart became increasingly less similar in salinity (Fig. 20). The scale of significant similarity was on the order of 25 km. Variables associated with the oysters themselves, like shell volume, biomass, and abundance, showed scales of patch size in the range of 10 to 15 km, a much smaller scale than observed with salinity (Fig. 20). A secondary, much weaker signal occurred in the 40 km range. Thus, similarity in oyster variables between sites only existed over short spatial scales, rarely more than one site removed from any given site. Measures of oyster condition, such as condition index, gonadal-somatic index and egg quantity, followed similar spatial trends (Fig. 20). Scales of similarity of *P. marinus* prevalence and infection intensity, crab abundance and mussel abundance were distinctly smaller, less than 10 km (Fig. 20). The four types of associated epibionts and endobionts, generally had longer scales of similarity, 15 to 20 km for bryozoans and barnacles and 10 to 15 km for algae and polychaetes (Fig. 20).

Results of directional autocorrelational analyses are reported in Figure 21. In general, the variables fell into three main groups. Directional trends for oyster density, crab density, juvenile and submarket-size density, and oyster biomass were similar to the distribution of shell volume which had a direction of similarity from 0.25 radians (14°) to 2.5 radians (143°), with a peak between 86° and 143° . The predominantly east-west orientation of similarity in these variables approximates the directional trend of the barrier reefs, which presumably follow the pre-1900 isohaline pattern of the bay prior to the creation of the ship channel. Salinity had a preferred orientation of 0.25 to 1.5 radians and 3.0 to 3.14 radians (14° to 86° , 171° to 180°), as did maximum clump size. This directional trend was substantially different from that observed for oyster density and shell volume. The dominant north-south component follows the trend of the isohalines that parallel the Houston Ship Channel. Gonadal-somatic index, egg quantity, *P. marinus* prevalence, algal coverage, box frequency, and polychaete abundance follow this isohaline pattern with a preferred direction of similarity between 3.0 and 3.14 radians (171° to 180° from N). Several other variables showed a trend diametric to salinity: condition index, bryozoan coverage, barnacle coverage (to some extent), mussel density, and, to some extent *P. marinus* infection intensity which also had attributes characteristic of the group defined by shell volume and oyster density. These variables had a predominant east-west direction of similarity in accordance with the direction of the primary barrier reef tracts and the pre-1900 isohaline structure, but the direction of similarity was much more focused than observed for oysters and shell volume.

Discussion

Spatial and directional structure

Both spatial scale and directional trends in spatial structure differed significantly among the variables assayed. Four spatial scales of similarity (akin to patch sizes) could be differentiated. Salinity had the longest spatial scale of similarity, about 25 km, followed by a variety of endobionts and epibionts at a slightly smaller scale of similarity, then oysters and associated measures defining condition, and finally predators, *P. marinus* and the mussel competitor. Three types of directional similarity were present; predominant trends parallel to the salinity isohalines, predominant trends perpendicular to the isohalines, and predominant trends determined, possibly, by the geological orientation of the reefs that presumably follow the pre-1900 isohaline structure of the bay.

Salinity was the primary structuring force in the bay. Cluster analyses, taking into account all measured variables, produced groupings primarily defined by salinity. Many of the directional trends were related to salinity and many of the variables had significant partial correlations with salinity or with other variables themselves significantly correlated with salinity. However, a considerable portion of the spatial structure was not explained by salinity. Two or more distinct groups were defined by cluster analysis within each broad salinity category. Most variables had spatial scales of similarity much smaller than did salinity. In effect, patch size extended over a significantly smaller area than explained by the local variation in salinity. Many variables had directional trends considerably different from salinity and, in fact, some had trends diametric to salinity. Accordingly, other factors were present that exerted a significant effect on the spatial structure of oyster reefs in Galveston Bay besides salinity.

One interesting feature of the spatial structure was the variation in scale of patch size between the oysters, crabs, *P. marinus*, and the mussel. The predator, parasite and competitor seemed to respond to factors other than oyster abundance or shell availability. The larger scale of patchiness suggests a more significant impact of salinity on these organisms than on the oysters themselves, which is a well-documented phenomenon.

Local versus regional control

Local factors exist that modify the spatial structure of oyster communities established within the regional salinity gradient. One such factor might be the degree of exploitation of the various reefs by the commercial fishery. Although the effect of the oyster fishery on oyster populations is controversial, shellfish harvesting can affect local community structure (e.g. Peterson et al., 1987). If the effect of the fishery was important, significant differences between open and closed areas should be present. Although all variables assayed varied considerably over the bay, none clearly varied with respect to whether the reefs were open or closed, with the possible exception of shell volume. Some closed reefs are fished during the summer relay season and others are not. In addition, the fishing effort on the open

reefs varies considerably among the reefs sampled. Accordingly, identifying subtle effects of the fishery in this data set is probably not possible. However, no overriding impact was observed based on the health-related variables assayed here and the accompanying reef survey did not identify any effect of the commercial fishery on reef accretion or loss. Furthermore, taking all factors into account, the healthiest reefs were in the most heavily-fished areas, so that no deleterious effect of the commercial fishery could be discerned in this study.

A second factor might be the availability of cultch material. Shell volume correlated best with oyster abundance and trends in directional similarity for shell volume and oyster abundance bore a strong resemblance to one another. However, many sites with available cultch had few adults and market-size abundance did not correlate nearly as well with shell volume as did total oyster abundance nor was the pattern of directional autocorrelation very similar. Probably, production on most reefs in the bay is not limited by shell availability and other factors than recruitment success are important in determining local productivity and survivorship to market size. However, shell budgets for these reefs have not been measured. Accordingly, the importance of shell availability in determining oyster abundance cannot be unequivocally evaluated.

Two important factors operative on spatial scales smaller than salinity which could affect community structure and health are current flow and food supply. The sites along the Houston Ship Channel differed from others of equivalent salinity in many regards for example, probably because current flow was higher. Sites west of the Houston Ship Channel and south of Todds Dump generally are lower in turbidity (our unpublished data). Lower turbidity, by increasing filtration rate, allows oysters to obtain more food (Powell et al., 1992b). Both turbidity and food supply were highly spatially variable and this variability did not necessarily follow the isohaline structure of the bay (our unpublished data). Many correlations, between for example juvenile abundance and gonadal-somatic index, suggest that some locations were more conducive to oyster production than others within a similar salinity regime. These data agree with the accompanying reef survey which showed that reefs accreting or losing area were not distributed solely with respect to salinity.

Model simulation

Simulation modeling was used to further define the reasons for the spatial distributions observed. The TAMU/ODU model was run using mean conditions of temperature and freshwater inflow, so that the simulation addressed the conditions in Galveston Bay that occur about 60% of the time rather than the flood conditions that were present during the sampling period. Nevertheless, the simulations showed considerable similarity to the field data collected.

The distribution of oyster abundance in the simulated population was similar to the observed distribution of oyster abundances. Highest abundances occurred on Redfish Bar and along the Houston Ship Channel (Fig. 22). The abundance of market-size oysters differed slightly between that observed in the field and that

calculated for the simulated population because the simulation contained a low salinity event in the San Jacinto portion of the bay. Accordingly, adult abundance was lower in the Buoy 75 to Morgans Point reach in the simulated population than observed. Otherwise, however, observed adult abundances were similar in the simulated population in Galveston Bay proper (Fig. 23). Higher production in the Deer Island area of West Bay, as compared to East Bay for example, is recorded in both the simulated population and the real data set. Similarly, low production in upper East Bay and the Clear Lake Embayment is observed in both cases and mortality due to low salinity is observed in Trinity Bay and along parts of Redfish Bar (Bowling 1992; Hofstetter, 1977). These trends are also present in biomass (Fig 24).

A final discrepancy between the simulated population and those observed in this study was the higher abundances in the Carancahua Reef area of West Bay and in the Pelican Island Embayment in the simulated populations. These higher abundances suggest that both areas are characterized by environmental conditions more satisfactory for oyster production than might be inferred from present densities. The observed absence of adult oysters and the presence of suitable cultch material suggests that an adequate larval supply does not exist under present conditions. Galtsoff (1931) records considerable production in the Pelican Island Embayment early in this century and suggests that the Texas City Dike was responsible for the deterioration of this fishery. The dike reduces current flow through the Pelican Island Embayment from Galveston Bay proper and would prevent a supply of larvae from the main portion of Galveston Bay from reaching this area. Furthermore, the tidal node for West Bay is now located near Carancahua Reef so that little net transport of water occurs upestuary or downestuary over this reef. Reduced current flow at Carancahua Reef can be inferred from the degree of siltation on the reef crest. No net water transport over Carancahua Reef might minimize larval transport to this area. On the other hand, larval recruitment is certainly adequate in the Deer Island area, but, then, current speeds are also locally higher around these reefs. Although some factor important in West Bay may not be included in the TAMU/ODU model, our data and simulation corroborate Galtsoff's (1931) view that the Texas City Dike has significantly reduced oyster production in West Bay by reducing water flow into West Bay from Galveston Bay proper.

Recognizing the absence of the Trinity River flood in the simulation, the distribution of the number of eggs produced among simulated populations (Fig. 25) was similar to the observed distribution in gonadal-somatic index. Thus, reefs with populations nearly ready to spawn in our samples, Redfish Bar, the Hanna Reef Tract, and the Houston Ship Channel reefs, produced more larvae in the simulated population. The lower gonadal-somatic indices in West Bay observed during our sampling correspond with the generally lower number of adult individuals, as previously discussed. The simulated populations once again suggest that the Pelican Island Embayment should be characterized by a higher fecundity than observed. Similarly the discrepancies in the simulated populations and those observed in Trinity Bay and the San Jacinto segment of Galveston Bay correspond with the variation in freshwater inflow pattern between the simulation and the year 1992.

The pattern of *P. marinus* prevalence and infection intensity differed considerably due to the variation in salinity regime between the simulated conditions and the conditions present prior to sampling in 1991/1992 (Figs. 26, 27). However, the endemism of *P. marinus* in the Deer Islands area of West Bay and the relatively high infection intensity in the Dickinson Embayment, particularly around April Fools Reef, is present in the simulated populations as is the relatively high infection intensities along the Houston Ship Channel.

Finally, the distribution of juveniles as observed agreed well with the simulated oyster populations. Most recruitment occurred along the Houston Ship Channel, on Redfish Bar, and the Todds Dump area. The simulation suggests a higher degree of recruitment than observed in West Bay, once again pointing to the failure of observation to agree with simulation in this area.

Temporal trends in health parameters

Oysters are susceptible to persistent population declines (Powell et al, in press). Changes in growth form and disease intensity (Lunz, 1938; Wade et al., 1992; Wilson et al., 1990) may be associated with environment degradation. Changes in food supply may also affect population abundance (Powell et al., submitted b; Ulanowicz and Tuttle, 1992). Unfortunately, climatic cycles, such as El Niño, also affect most of the measured variables (Powell et al., 1992; Wilson et al., 1992), as they do most shellfish (Hettler, 1992; Childers et al., 1990). Although previous measurements of many of these parameters exist for Galveston Bay (e.g. Soniat et al., 1989), a long-term data set sufficient to distinguish unidirectional changes due to environmental degradation or improvement from changes produced by climatic cycles does not exist. As an example, the comparison made between the measurements of Soniat et al. (1989), Choi et al. (1993), Powell et al. (1992a), and those reported here (Tables 5-7) show substantial variations in abundance and health; however it is likely that these can be attributed, at least in part, to the El Niño cycle. The current sampling was conducted during an El Niño (Halpert and Ropelewski, 1993; NOAA, 1989) whereas the sampling of Soniat et al. (1989) took place during a La Niña period, the sampling of Choi et al. (1989) during a transition phase, and the sampling of Powell et al. (1992a) during both El Niño and La Niña periods. Freshwater inflows normally vary considerably between the two extremes (Kahya and Dracup, 1993). The variations observed, then, could easily be produced by simple climate variation.

Further complicating these comparisons is the problem associated with false negatives in the *P. marinus* analyses. Hofmann et al. (submitted) and Choi et al. (1989) discussed the occurrence of false negatives using the standard thioglycollate technique. In this study, the use of a quantitative technique for all suspected negative infections increased prevalence substantially. False negatives were common and, unfortunately, relatively more common at some sites than others in comparison to what might be inferred from the infection intensity of individuals recorded as positive by the standard thioglycollate method. Comparisons in Tables 5 and 7 were made using the results of the standard assay which considerably

underestimates prevalence and infection intensity. The degree to which false negatives occur is not easy to ascertain, then, yet they exert a significant impact on infection intensity as standardly calculated.

Hofmann et al. (submitted) also showed that the results of *P. marinus* analyses will be crucially dependent on the size and age structure of the sampled population. Variations in prevalence and infection intensity are partly controlled by environmental conditions and partly controlled by community history, the history of introduction of uninfected individuals, disease transmission and mortality (Hofmann et al., submitted). In our samples, prevalence and infection intensity varied considerably among size classes. As this size and age structure changes from year to year and is rarely recorded in reports of *P. marinus* prevalence and infection intensity, important questions concerning the temporal trends in population health cannot be answered without a long-term data set and careful control of the size classes assayed. Thus insufficient data presently exist to differentiate climatic and stochastic changes from true unidirectional trends.

Predation versus disease

One of the interesting aspects of population dynamics is the likely relative importance of predators, competitors and diseases in controlling oyster production. Simulations can be used to assess the potential importance of these agents of mortality and morbidity in Galveston Bay. Simulations using the density and size frequency of mussels encountered in this study suggest that mussel densities are generally too low to restrict food availability under the current flow regime and food supply presently available in Galveston Bay. Comparison of *P. marinus*-induced and predator-induced mortality, using the densities and size-frequencies of the predators as observed and initializing the model with the measured *P. marinus* prevalences, suggests that the two sources of mortality share about an equal proportion of yearly mortality, based on abundance, over the entire bay. Of course, in certain areas, one source of mortality is relatively more important than another. The predators, however, prey predominantly on the smaller size classes. Accordingly, based on biomass, *P. marinus* has a much more significant effect and probably accounts for much of the natural mortality in the market-size fraction of most populations, as suggested by Hofstetter (1977), and represents a significant factor in restricting and structuring fecundity in the bay.

Conclusions

Examination of the spatial structure of community and health-related variables of Galveston Bay oyster populations reveals that factors other than salinity play an important role in determining the status of individual populations. The factors, current flow and food supply being likely candidates, create patch sizes of 10 to 15 km in extent and produce directional trends that frequently do not run perpendicular to salinity isohalines. The results of this onetime spatially-intensive survey corroborate the integrated picture from an assessment of the 20-year trends in reef accretion and loss which suggested that selected areas of the bay have a

much higher inherent productivity than other areas. Many of these areas are in the moderate to high salinity regions of the bay. This inherently higher productivity occurs despite higher predator abundance and significantly higher prevalence and infection intensity of *P. marinus* at these sites.

Three sets of data, the accompanying reef survey, the present health survey, and the simulation, suggest that the most productive regions of Galveston Bay under most conditions are the South Redfish Reef/Dickinson Embayment area, the reefs adjacent to the Houston Ship Channel southeast of Buoy 75, the Bull Hill area of the Hanna Reef Tract, and to some extent the Deer Islands/Confederate Reef area of West Bay. These four areas accreted the most reef in the Galveston Bay system over the last 20 years, they were observed to be the most productive areas under the conditions of the simulation (mean monthly freshwater inflow and mean daily temperature), and they generally produced the healthiest oyster populations in the health assessment, as measured by density, size-frequency distribution, and gonadal state. Both the health assessment and the simulation suggest that the South Redfish Reef and Houston Ship Channel area could be a principle location for brood stock in Galveston Bay.

As one final check, we ranked the 51 sites according to five variables directly related to condition: oyster abundance, oyster biomass, gonadal-somatic index, *P. marinus* infection intensity, and condition index. Each site was given a weight from 1 (best) to 51 (worst) according to their position when ranked among the 51 (Table 9). Fifteen of the seventeen top sites are along Redfish Bar, the Houston Ship Channel or in the Dickinson Embayment. Sites in West Bay, Trinity Bay, and upper East Bay normally ranked in the lower third of all the sites. These rankings agree with the model and with the reef survey.

Comparison of the field data and the model simulation also shows that the most important discrepancy between observation and expectation occurs in the Pelican Island Embayment and central West Bay. Whether due to restricted larval availability or some unidentified source of environmental degradation, this area is currently supporting much lower production than would be expected from known conditions or which was observed previously (Galtsoff, 1931). Probably, the Texas City Dike is responsible for at least a portion of this discrepancy.

Finally it is interesting to note that the Redfish Bar area under pre-1900 conditions was not productive (Galtsoff, 1931). The reef was too shallow and production was limited by current flow and a sharp salinity gradient. Most dredged channels are responsible for significant local changes in isohaline structure (e.g. Raney, 1988; Counts and Bashore, 1991). The productivity of the central part of Galveston Bay from the Dickinson Embayment across the Redfish Bar Reef Tract would appear to be the result of the dredging of the Houston Ship Channel and the gradual expansion of reefs parallel to the new isohaline structure of the bay. The data and model simulation demonstrate that local factors, probably related to food supply and current flow, can override the negative effects of increased mortality due to predation and disease and permit the production of healthy oyster populations in relatively moderate to high salinity areas. The region of highest inherent productivity in the bay, and also the region of greatest reef accretion, exists in the